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Dental Development in Chimpanzees (*Pan troglodytes*): The Timing of Tooth Calcification Stages

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ABSTRACT Data are presented documenting the timing of tooth calcification for the left mandibular dentition (I_1–M_3) based on a cross-sectional series of intraoral dental X-rays from a sample of 118 captive chimpanzees. Mean, median, and midpoint ages of attainment; standard deviations (SD); interquartile ranges (IQR); and age ranges were calculated for the eight developmental stages of these teeth. Minor differences with previous studies of chimpanzee dental development were found (Anemone et al. [1991] Am. J. Phys. Anthropol. *86:*229–241; Anemone and Watts [1992] J. Hum. Evol. *22:*149–153), but the similarities with previous studies are more striking despite the differences in samples. In contrast to other pongid studies, sex differences in developmental timing were documented, particularly for the canine. Regression models for age estimation from dental maturity scores were also presented. This chimpanzee standard is compared with human standards to determine absolute and relative differences in the timing of crown and root calcification. The overall period of canine development in both species is nearly identical, although those for crown and root formation are markedly different—making this tooth the most distinctive feature between chimpanzee and human dental development periods. Although the molars demonstrate differences in the timing of crown and root calcification periods, they are more proportional than for other teeth. This contributes to the difficulties in distinguishing between "human" and "chimpanzee" patterns of molar development. The developmental differences discussed are placed in perspective with consideration to microstructural and morphological features of chimpanzee and human teeth, and to overall growth periods in these species.

One recent focus in reconstructions of the life history of ancestral hominids (particularly the australopithecines) concerns whether they followed a modern, human-like, prolonged schedule of growth and development (Mann, 1975, 1988; Dean, 1985, 1987; Smith, 1986, 1989a,b, 1991b; Bromage, 1987; Conroy and Vannier, 1987, 1988, 1991a,b; Mann et al., 1987, 1990, 1991; Conroy, 1988; Wolpoff et al., 1988). Part of this debate has centered around comparisons of the pattern and timing of tooth development (calcification and emergence) between modern humans and pongids (Dean and Wood 1981; Bromage and Dean 1985; Simpson et al., 1990, 1991, 1992; Anemone et al., 1991; Conroy and Mahoney 1991; Anemone and Watts 1992; Kuykendall 1992; Kuykendall et al., 1992), which are used as comparative models for assessing hominid fossils. Al-

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though a number of criteria claimed to distinguish between pongids and humans have been identified and applied to the fossil record (e.g., Mann, 1975, 1988; Smith, 1986, 1987a,b, 1989a,b; Conroy and Vannier, 1987, 1988, 1991a,b; Conroy, 1988; Mann et al., 1987, 1990, 1991), a consensus among these studies has not been reached because of a lack of adequate comparative data.

Although some data have been published documenting various aspects of dental development in chimpanzees and other pongids (Dean and Wood, 1981; Swindler, 1985; Simpson et al., 1990, 1991, 1992; Anemone et al., 1991; Beynon et al., 1991; Siebert and Swindler, 1991; Winkler et al., 1991; Anemone and Watts, 1992), such studies to date have been wanting with regards to some or all of the following: a) adequate sample sizes for living subjects of known age and sex in a single pongid species; b) radiographic procedures designed to procure data for all tooth types in at least one jaw; c) documentation and/or discussion of sex differences in the timing of tooth calcification stages; and d) analysis of individual variation in the pattern and timing of crown and root calcification, *in addition* to population norms for sequences of tooth calcification and ages for tooth calcification stages. Further problems limiting comparisons among existing studies are the discrepancies between samples, analytical techniques, and presentation of results (Smith, 1991a, discussed these issues with respect to human studies). As a result of these problems, many lingering questions remain unanswered concerning differences in dental development between modern pongids and humans.

The primary aim of research presented in this paper is to assess new basic data documenting the timing of tooth crown and root calcification stages for a single pongid species (*Pan troglodytes*).

MATERIALS AND METHODS

The study sample was composed of 118 captive chimpanzees of known age and sex, housed at the laboratory for Experimental Medicine and Surgery In Primates (LEMSIP) at New York University (NYU) Medical Center, and the Yerkes Regional Primate Research Center at Emory University, Atlanta. This included 60 females and 58 males, which ranged in age at the time of the study from 1.5 months to 10 years and 9 months (Table 1). All yearly age groups up to 12 years (e.g., 0–1 years, 1–2 years) were represented in this sample, but there were no females between 10 and 11 years at either facility. Also, there were no females from Yerkes between 3 and 4 or 7 and 8 years, and no males from Yerkes between 5 and 6 or 8 and 9 years.

Radiographs were collected using standard periapical intraoral and extraoral techniques (see Frommer, 1981). Collection of X-rays was limited to the left mandibular dentition because a) obtaining undistorted X-rays of the maxillary dentition is hindered by the shallow palatal arch in chimpanzees; b) reported differences in tooth emergence and development between the maxillary and mandibular pairs, or between right and left antimeres, are reportedly not statistically significant in either humans or chimpanzees (Nissen and Riesen, 1964; Dean and Wood, 1981; Demirjian, 1979; Kuykendall et al., 1992); and c) there are potential health risks to the chimpanzees if they are anaesthetized for more lengthy radiographic procedures.

The X-rays were collected using a Min-X-Ray P200D Portable Dental X-ray Unit with nonadjustable power settings of 12 mA at 63 KVP, and a standard 6 inch dental cone for all procedures. X-ray exposure times ranged from 0.25 to 0.5 seconds for periapical and occlusal films, and 0.3 to 2.0 seconds for extraoral lateral obliques.

The analysis of tooth calcification status from these X-rays followed an eight-stage scoring system (Table 2) similar to those used previously by Demirjian et al. (1973; also Demirjian and Levesque, 1980) and others (Fleagle and Schaffler, 1982; Anemone et al., 1991; Conroy and Vannier, 1991b). Some modifications in stage definitions were made because of differences in chimpanzee tooth morphology (compared to humans), and to make the stage assessments more objective. Defining criteria for each stage were based on discrete traits describing the shape and appearance of observable features, rather than on linear measurements. Fractional stages of crown and root formation have been utilized in some studies (e.g., Nolla, 1960;

TABLE 1. *Summary of study sample by facility, age, and sex*[1]

Age category	LEMSIP			Yerkes			Total		
	Males	Females	Totals	Males	Females	Totals	Males	Females	Totals
0–1	4	4	8	1	1	2	5	5	10
1–2	4	7	11	3	3	6	7	10	17
2–3	2	4	6	2	2	4	4	6	10
3–4	7	5	12	1	0	1	8	5	13
4–5	3	2	5	3	1	4	6	3	9
5–6	5	2	7	0	2	2	5	4	9
6–7	2	5	7	3	3	6	5	8	13
7–8	4	9	13	2	0	2	6	9	15
8–9	5	5	10	0	3	3	5	8	13
9–10	1	1	2	2	1	3	3	2	5
10–11	2	0	2	2	0	2	4	0	4
Totals	39	44	83	19	16	35	58	60	118

[1] The sample includes 6 chimpanzees from LEMSIP for whom dates of birth are known only to the year. These individuals were excluded from all statistical calculations requiring accurate ages at the examination date.

Fanning, 1961; Moorrees et al., 1963; Fanning and Brown, 1971; Dean and Wood, 1981), but are not considered to be reliable without sequential X-rays from longitudinal data (Garn et al., 1957; Demirjian, 1986), and thus were avoided here.

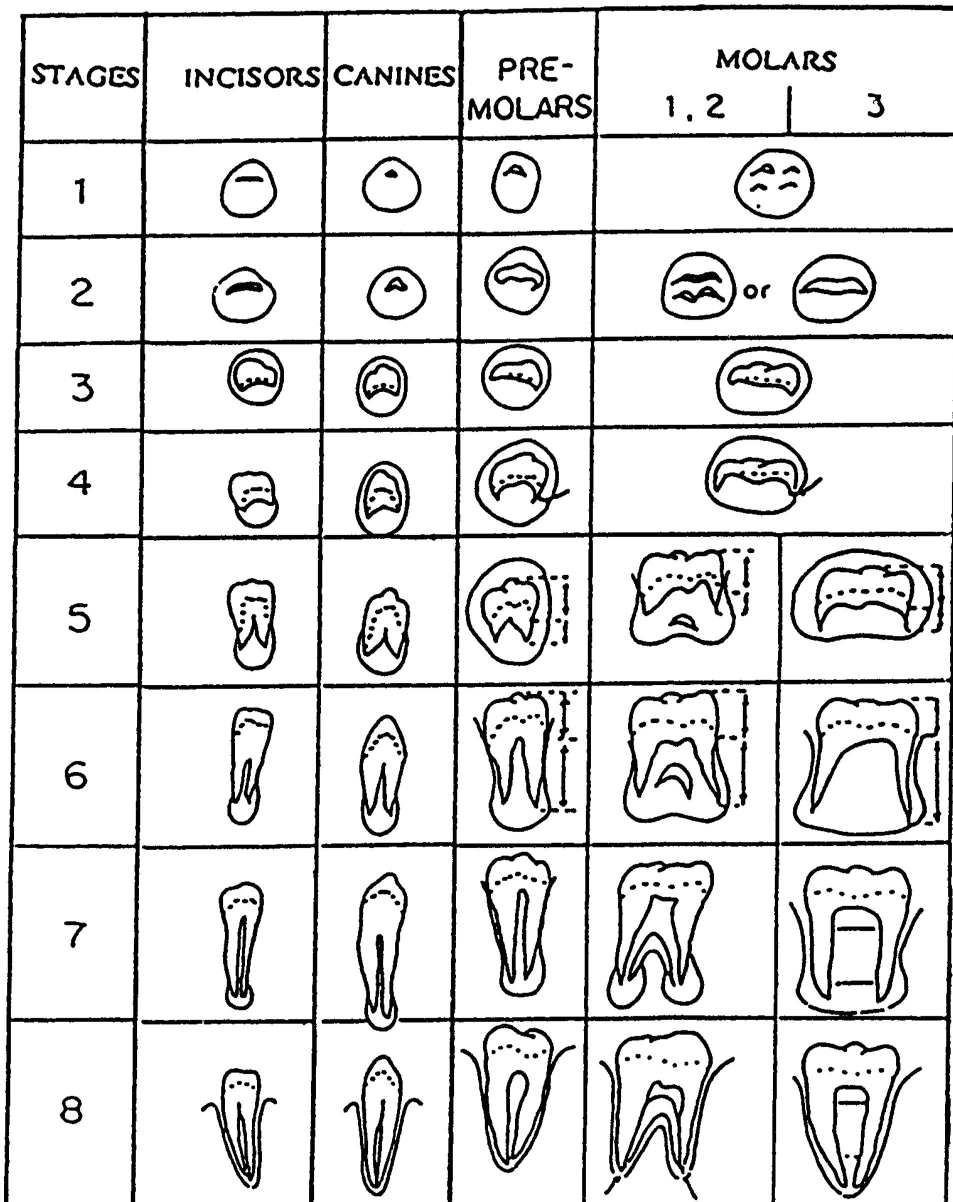
The status of tooth calcification was assessed in each radiograph in two separate trials by the same observer; no differences between first and second trials were greater than one stage. Those teeth (i.e., from particular X-rays) demonstrating different scores between trials were re-examined to resolve their scores and thus generate the final data set.

Population standards for dental development may represent either the average "age for stage" (e.g., Moorrees et al., 1963; Dean and Wood, 1981; Anemone et al., 1991), or the average (mean or modal) "stage for age" (Nolla, 1960; Nanda and Chawla, 1966; Sapoka and Demirjian, 1971). Both types of developmental standards have been presented for humans, but to date, only the former exist for chimpanzees. This study presents both types of developmental standards for chimpanzees.

Summary statistics were generated to establish "age for stage" population norms for the timing of tooth development stages. Three estimates of centrality for the age at each developmental stage (per tooth) are presented—means, medians, and midpoint ages of attainment (or MA age). The third measure was calculated as the average age between the oldest chimpanzee having attained a given stage, and the youngest chimpanzee not having attained that stage (see Phillips-Conroy and Jolly, 1988; Smith, 1991a). These MA age estimates approximate the typical age at attainment (or "age-at-entry") of a given developmental stage. As such, they are similar in nature to results from probit or cumulative distribution functions (though less sophisticated), and are useful for construction of a standard developmental chronology (Smith, 1991a). Ages at attainment are generally younger (and fundamentally different) than "in-stage" age estimates such as medians and means, which represent the "average" age of all chimpanzees *already exhibiting* a particular stage of development (Eveleth and Tanner, 1976; Smith, 1991a). "Stage for age" standards were generated simply by calculating the modal stage for each yearly age group from 0 to 11 years.

The Wilcoxon rank-sum test (a nonparametric alternative to the t-test) and the Bonferroni correction (in a one-way analysis of variance) were utilized to examine data for statistically significant sex differences in age during tooth development. For the Wilcoxon results, statistical significance was defined at $P < 0.05$. The Bonferroni test was included because eight Wilcoxon rank-sum tests are made for each tooth (i.e., there are multiple tests because there are eight developmental stages per tooth), which increases the chance of falsely rejecting the null hypothesis (Type I error). This alternative test essentially divides the specified P-value by the number of comparisons being made, so that a difference must obtain a very small P-

TABLE 2. *Stages of dental development*[1]



(*continued*)

value to claim statistical significance. With eight comparisons per tooth, the significance level required in the Bonferroni tests was thus $P < 0.0063$.

Dental maturity status was utilized to predict age using two different polynomial regression models. Dental maturity scores were calculated as the sum of an individual's tooth stage scores. The calculations in the first model (DM) used all eight teeth and ranged in value from 0 to 64 (8 stages of 8 teeth); the second (Dm) calculation omitted M_3 because of the high incidence of missing data, and ranged in value from 0 to 56.

TABLE 2. Stages of dental development[1] *(continued)*

Stage	Description
1	In both uniradicular and multiradicular teeth, the initial calcification is visible in the superior region of the tooth crypt as one or a series of inverted cones; there is no fusion of these calcified points
2	Fusion of the calcified points forms one or several cusps which unite to give a regularly outlined occlusal surface
3	a) Enamel formation is complete at the occlusal surface. Its extension and convergence towards the cervical region is visible
	b) Beginning of a dentinal deposit is present below the enamel crown
	c) The outline of the pulp chamber has a curved shape at the occlusal border
4	a) Crown formation is complete to the cementoenamel junction
	b) The superior border of the pulp chamber in uniradicular teeth has a definite curved form, being concave toward the cervical region; if the pulp horns are present, they give an outline like an umbrella top. In molars, the pulp chamber has a trapezoidal form
	c) Beginning of root formation is observable in the form of a spicule
5	Uniradicular teeth:
	a) The walls of the pulp chamber form straight lines, but may be interrupted by the presence of pulp horns
	b) Root length is less than crown height
	Premolars and molars:
	a) Initial formation of the radicular bifurcation is visible as either a calcified point, or a semilunar mass
	b) Root length is still less than crown height
6	Uniradicular teeth:
	a) The walls of the pulp chamber approximate an isosceles triangle. The apex ends in a funnel shape
	b) Root length is equal to or greater than the crown height
	Molars:
	a) The calcified region of the bifurcation has developed further down from its semilunar stage to give more definition to the roots, which have funnel-shaped endings
	b) The root length is equal to or greater than the crown height
7	a) The walls of the root canals are parallel (distal root in molars)
	b) The apical ends of the root canal are open, but NOT funnel-shaped; the periodontal membrane bulges around the root apices
	c) Proximal and distal roots of multiradicular teeth are parallel—root elongation is complete
8	a) The apical end of the root canal is completely closed (distal root in molars)
	b) The periodontal membrane has a uniform width around the roots and apices
	c) In multiradicular teeth, the roots may converge distally

[1] Definitions of tooth formation stages derived from Demirjian et al. [1973]

Regression models using a transformed (squared) independent variable (e.g., DM^2) provided the best fit to the data. For the polynomial equations, estimates for plus- and minus-two standard deviations at the mean dental maturity score were calculated as twice the model Root Mean Square Error (obtained from the computer-generated output for a particular regression model); 95% confidence bands for the regression graphs provided were estimated as twice the standard error of the predicted ages (also obtained from the statistics package; Computing Resource Center, 1989).

Finally, a graphical comparison of tooth calcification periods in chimpanzees and humans was produced (see Results for details).

RESULTS

Summary statistics

Table 3 presents summary statistics for the timing of tooth development in this sample of chimpanzees, including separate tables for males and females (Table 3b,c). Note that data for the canine are available only to stage 7, and for M_3 only to stage 6. Mean and median ages at each of the eight stages for each tooth were compared as an informal measure of skewness (Hamilton, 1990). Both positively (mean > median) and negatively skewed (mean < median) distributions were found, although none of the mean and median ages differ by more than 0.5 years. Although these data do not appear to be highly skewed, sample sizes and age distributions are highly variable among tooth stages; thus medians are the preferable statistic for centrality in age.

Standard deviations (SD) and interquartile ranges (IQR) are presented in Table 3 for the mean and median ages, respectively, of each developmental stage. Both of these parameters indicate similar patterns for variability in timing of tooth development; later-occurring events are more variable (i.e., greater dispersion about the mean/

TABLE 3. Summary statistics for chimpanzee dental development (a), and for male (b) and female (c) chimpanzees[1]

Tooth/ stage	No. Obs.	Median (50th)	IQR (25th–75th)	Mean	SD	MA	Range
a. Chimpanzee dental development							
I1							
1	3	0.48	·	0.48	0.03	0.42	0.45–0.51
2	2	0.63	·	0.64	0.23	0.49	0.47–0.80
3	29	1.58	1.32–2.19	1.79	0.69	0.74	0.69–3.37
4	15	3.45	3.23–4.61	3.80	0.74	3.13	2.89–5.05
5	7	4.95	4.61–5.22	4.84	0.48	4.49	3.93–5.36
6	20	6.22	5.81–6.44	6.17	0.70	4.97	4.58–7.69
7	21	7.74	7.63–8.15	7.93	0.68	7.31	6.92–9.30
8	9	9.55	8.57–10.12	9.41	1.01	8.64	7.99–10.75
I2							
1	3	0.48	·	0.48	0.03	0.42	0.45–0.51
2	1	(0.47)	·	·	·	0.49	·
3	31	1.57	1.31–2.19	1.74	0.70	0.58	0.69–3.37
4	15	3.45	3.23–4.61	3.80	0.74	3.13	2.89–5.05
5	9	4.95	4.61–5.22	4.89	0.50	4.49	3.93–5.60
6	19	6.31	6.04–6.50	6.35	0.65	5.43	5.27–7.69
7	24	8.04	7.66–8.86	8.15	0.84	7.31	6.92–10.12
8	5	9.69	8.57–10.73	9.62	1.14	9.24	8.35–10.75
C							
1	4	0.48	0.46–0.50	0.48	0.03	0.42	0.45–0.51
2	14	1.26	1.00–1.36	1.18	0.26	0.60	0.69–1.48
3	48	3.44	2.62–5.00	3.81	1.50	1.46	1.44–7.04
4	10	6.39	6.06–6.96	6.62	0.79	6.32	5.60–8.20
5	17	7.66	7.25–7.78	7.63	0.61	7.19	6.19–8.75
6	11	9.30	8.35–10.12	9.32	0.96	8.37	7.99–10.75
7	1	(9.22)	·	(9.22)	·	9.97	·
8	·	·	·	·	·	·	·
P3							
1	8	1.47	1.44–1.65	1.52	0.14	1.34	1.31–1.73
2	4	1.66	1.58–1.89	1.73	0.22	1.65	1.57–2.04
3	20	3.21	2.62–3.33	3.01	0.49	2.09	2.14–3.82
4	12	4.67	4.47–5.01	4.72	0.41	3.87	3.93–5.36
5	7	5.78	5.28–6.04	5.67	0.54	5.05	4.73–6.41
6	26	7.06	6.37–7.73	7.04	0.80	5.84	5.27–8.20
7	9	8.57	7.69–9.22	8.53	0.77	7.91	7.63–9.55
8	7	9.69	8.35–10.73	9.51	1.11	8.77	7.99–10.75
P4							
1	6	1.47	1.44–1.60	1.50	0.13	1.37	1.31–1.69
2	5	1.73	1.58–1.75	1.73	0.19	1.63	1.57–2.04
3	21	3.23	2.62–3.35	3.11	0.69	2.09	2.14–5.36
4	11	4.61	4.29–4.95	4.60	0.54	4.58	3.81–5.78
5	6	5.25	5.07–6.04	5.46	0.64	5.25	4.73–6.41
6	27	6.96	6.25–7.69	6.93	0.85	5.84	5.27–8.15
7	13	8.75	7.78–9.22	8.61	0.87	7.67	7.14–10.12
8	5	9.69	8.35–10.73	9.50	1.30	9.06	7.99–10.75
M1							
1	1	(0.13)	·	(0.13)	·	(0.13)	·
2	4	0.46	0.42–0.49	0.46	0.05	0.26	0.39–0.51
3	14	1.31	1.00–1.43	1.21	0.28	0.60	0.69–1.60
4	9	1.69	1.57–1.75	1.69	0.30	1.40	1.21–2.19
5	7	2.61	2.46–3.26	2.72	0.46	2.17	2.14–3.42
6	16	3.33	3.21–4.06	3.63	0.80	3.02	2.62–5.36
7	27	5.84	4.95–6.37	5.75	1.12	4.58	3.80–8.10
8	30	8.14	7.66–8.97	8.30	1.12	7.29	6.47–10.75
M2							
1	7	1.31	1.21–1.45	1.34	0.13	1.29	1.15–1.48
2	8	1.71	1.59–1.89	1.81	0.32	1.53	1.57–2.49
3	20	3.23	2.78–3.40	3.21	0.59	2.34	2.19–4.61
4	7	4.73	3.93–5.05	4.59	0.59	4.20	3.81–5.36
5	7	5.07	4.73–5.78	5.20	0.53	4.99	4.61–6.04
6	30	6.71	6.19–7.66	6.78	0.96	5.31	4.58–8.20
7	17	8.75	7.99–9.30	8.74	0.97	7.67	7.14–10.75
8	1	(10.73)	·	·	·	10.74	(10.73)

(continued)

TABLE 3. Summary statistics for chimpanzee dental development (a), and for male (b) and female (c) chimpanzees[1] (continued)

Tooth/ stage	No. Obs.	Median (50th)	IQR (25th–75th)	Mean	SD	MA	Range
M3							
1	5	3.23	3.23–3.42	3.50	0.64	3.41	2.99–4.61
2	7	4.36	3.93–4.95	4.45	0.52	4.20	3.81–5.22
3	18	6.28	5.07–6.92	6.08	0.98	4.85	4.58–7.69
4	8	7.53	6.08–8.10	7.28	0.88	6.88	6.06–8.15
5	13	8.13	7.73–8.97	8.35	0.78	7.65	7.14–9.69
6	5	10.12	9.55–10.73	10.02	0.77	9.33	8.97–10.75
7	·	·	·	·	·	·	·
8	·	·	·	·	·	·	·
b. Male chimpanzees							
I1							
1	1	(0.45)	·	(0.45)	·	(0.42)	·
2	1	(0.80)	·	(0.80)	·	(0.62)	·
3	12	1.59	1.40–2.33	1.80	0.56	0.90	1.00–2.67
4	10	3.81	3.42–4.61	3.95	0.65	2.94	3.20–4.95
5	4	5.14	4.50–5.29	4.90	0.66	4.44	3.93–5.36
6	8	6.17	5.52–6.37	5.90	0.66	4.97	4.58–6.47
7	9	7.78	7.73–8.20	8.03	0.66	6.76	7.04–9.30
8	5	10.12	9.55–10.73	9.95	0.91	8.94	8.57–10.75
I2							
1	1	(0.45)	·	(0.45)	·	(0.42)	·
2	·	·	·	·	·	·	·
3	13	1.58	1.36–2.04	1.72	0.61	0.80	0.80–2.67
4	10	3.81	3.42–4.61	3.95	0.65	2.94	3.20–4.95
5	5	5.07	4.58–5.22	4.83	0.59	4.44	3.93–5.36
6	7	6.25	5.78–6.37	6.08	0.43	5.32	5.27–6.47
7	11	8.10	7.74–8.75	8.36	0.95	6.76	7.04–10.12
8	3	10.73	·	10.02	1.25	9.35	8.57–10.75
C							
1	1	(0.45)	·	(0.45)	·	(0.42)	·
2	5	1.32	1.00–1.36	1.18	0.27	0.62	0.80–1.43
3	30	4.11	3.20–5.27	4.16	1.55	1.50	1.57–7.04
4	2	7.28	·	7.28	1.29	6.71	6.37–8.20
5	6	7.76	7.73–8.57	8.04	0.49	7.93	7.66–8.75
6	5	10.12	9.55–10.73	10.09	0.66	9.03	9.30–10.75
7	·	·	·	·	·	·	·
8	·	·	·	·	·	·	·
P3							
1	2	1.52	·	1.52	0.12	1.40	1.43–1.60
2	4	1.66	1.58–1.89	1.73	0.22	1.59	1.57–2.04
3	9	3.23	2.67–3.42	3.18	0.47	2.33	2.61–3.82
4	10	4.67	4.36–5.07	4.71	0.45	3.87	3.93–5.36
5	1	(5.78)	·	(5.78)	·	(5.57)	·
6	13	7.04	6.37–7.74	7.01	0.93	5.52	5.27–8.20
7	3	9.30	·	9.14	0.51	8.38	8.57–9.55
8	3	10.73	·	10.53	0.36	9.84	10.12–10.75
P4							
1	1	(1.60)	·	(1.60)	·	(1.52)	·
2	4	1.66	1.58–1.89	1.73	0.22	1.59	1.57–2.04
3	10	3.24	2.67–3.45	·	0.81	2.33	2.61–5.36
4	9	4.58	4.29–4.73	4.56	0.59	4.58	3.80–5.78
5	2	5.14	5.07–5.22	5.14	0.11	5.42	5.07–5.22
6	11	6.47	6.25–7.74	6.87	0.94	5.52	5.27–8.20
7	7	8.75	7.78–9.55	8.83	0.89	7.97	7.74–10.12
8	2	10.74	·	10.74	0.02	10.43	10.73–10.75
M1							
1	1	(0.13)	·	(0.13)	·	(0.13)	·
2	2	0.42	·	0.42	0.04	0.26	0.39–0.45
3	6	1.34	0.20–1.43	1.25	0.30	0.62	0.80–1.60
4	4	1.66	1.58–1.89	1.73	0.22	1.59	1.57–2.04
5	4	2.96	2.64–3.34	2.99	0.41	2.33	2.61–3.42
6	8	3.63	3.21–4.51	3.84	0.91	3.02	2.62–5.36
7	13	5.22	4.61–6.37	5.53	1.34	4.58	3.80–8.10
8	13	8.57	7.74–9.55	8.67	1.36	7.29	6.47–10.75

(continued)

TABLE 3. Summary statistics for chimpanzee dental development (a), and for male (b) and female (c) chimpanzees[1] *(continued)*

Tooth/ stage	No. Obs.	Median (50th)	IQR (25th–75th)	Mean	SD	MA	Range
M2							
1	·	·	·	·	·	·	·
2	5	1.60	1.58–1.75	1.71	0.20	1.57	1.57–2.04
3	11	3.26	2.67–3.82	3.39	0.66	2.33	2.61–4.61
4	6	4.51	3.93–4.95	4.51	0.61	4.20	3.81–5.36
5	3	5.22	·	5.35	0.37	5.22	5.07–5.78
6	13	6.47	6.25–7.73	6.76	1.11	5.18	4.58–8.20
7	7	9.30	8.57–10.12	9.25	1.01	7.97	7.74–10.75
8	1	(10.73)	·	(10.73)	·	(10.74)	·
M3							
1	3	3.42	·	3.75	0.75	3.53	3.23–4.61
2	6	4.33	3.93–4.95	4.43	0.56	4.20	3.80–5.22
3	8	6.37	5.17–6.76	6.10	1.05	4.90	4.58–7.66
4	3	7.78	·	7.32	1.09	6.87	6.08–8.10
5	5	8.57	7.74–8.75	8.42	0.68	7.92	7.73–9.30
6	4	10.42	9.84–10.74	10.29	0.57	9.43	9.55–10.75
7	·	·	·	·	·	·	·
8	·	·	·	·	·	·	·
c. Female chimpanzees							
I1							
1	2	0.50	·	0.50	0.02	0.48	0.48–0.51
2	1	(0.47)	·	(0.47)	·	(0.49)	·
3	17	1.48	1.31–2.19	1.79	0.78	0.58	0.69–3.37
4	5	3.23	2.99–3.31	3.50	0.89	3.13	2.89–5.05
5	3	4.73	·	4.76	0.17	4.83	4.61–4.95
6	12	6.25	5.94–6.73	6.34	0.69	5.11	5.28–7.69
7	12	7.68	7.33–8.15	7.86	0.71	7.31	6.92–9.22
8	4	8.66	8.17–9.33	8.75	0.75	8.61	7.99–9.68
I2							
1	2	0.50	·	0.50	0.02	0.48	0.48–0.51
2	1	(0.47)	·	(0.47)	·	(0.49)	·
3	18	1.47	1.21–2.19	1.75	0.77	0.58	0.69–3.37
4	5	3.23	2.99–3.31	3.50	0.89	3.13	2.89–5.05
5	4	4.84	4.67–5.27	4.97	0.44	4.83	4.61–5.60
6	12	6.36	6.05–7.10	6.50	0.72	5.44	5.28–7.69
7	13	7.99	7.63–8.15	7.98	0.74	7.31	6.92–9.22
8	2	9.02	8.35–9.69	9.02	0.95	8.79	8.35–9.69
C							
1	3	0.48	·	0.49	0.02	0.47	0.47–0.51
2	9	1.21	1.15–1.31	1.18	0.26	0.60	0.69–1.48
3	18	3.11	2.19–4.61	3.22	1.24	1.46	1.44–5.28
4	8	6.36	6.05–6.73	6.45	0.64	5.44	5.60–7.69
5	11	7.53	7.08–7.69	7.40	0.57	6.94	6.19–8.15
6	6	8.66	8.13–8.97	8.68	0.64	8.07	7.99–9.69
7	1	(9.22)	·	(9.22)	·	(9.46)	·
8	·	·	·	·	·	·	·
P3							
1	6	1.47	1.44–1.69	1.52	0.16	1.31	1.31–1.73
2	·	·	·	·	·	·	·
3	11	2.99	2.46–3.31	2.88	0.48	2.14	2.14–3.37
4	2	4.78	4.61–4.95	4.78	0.24	4.00	4.61–4.95
5	6	5.72	5.28–6.04	5.65	0.59	4.84	4.73–6.41
6	13	7.08	6.50–7.53	7.07	0.69	6.23	6.06–8.15
7	6	7.91	7.66–8.97	8.22	0.71	7.89	7.63–9.22
8	4	8.66	8.17–9.33	8.75	0.75	8.61	7.99–9.69
P4							
1	5	1.45	1.44–1.48	1.48	0.14	1.31	1.31–1.69
2	1	(1.73)	·	(1.73)	·	(1.71)	·
3	11	2.99	2.46–3.31	2.88	0.48	1.94	2.14–3.37
4	2	4.78	4.61–4.95	4.78	0.24	4.00	4.61–4.95
5	4	5.66	5.00–6.22	5.61	0.76	4.84	4.73–6.41
6	16	7.02	6.25–7.66	6.97	0.81	6.00	5.60–8.15
7	6	8.55	7.66–8.97	8.35	0.84	7.65	7.14–9.22
8	3	8.35	7.99–9.69	8.67	0.90	8.61	7.99–9.69

(continued)

TABLE 3. Summary statistics for chimpanzee dental development (a), and for male (b) and female (c) chimpanzees[1] (continued)

Tooth/ stage	No. Obs.	Median (50th)	IQR (25th–75th)	Mean	SD	MA	Range
M1							
1	·	·	·	·	·	·	·
2	2	0.49	·	0.49	0.03	0.47	0.47–0.51
3	8	1.26	1.00–1.38	1.18	0.28	0.60	0.69–1.48
4	5	1.69	1.44–1.73	1.65	0.37	1.34	1.21–2.19
5	3	2.46	2.14–2.49	2.36	0.19	2.17	2.14–2.49
6	8	3.28	3.11–3.36	3.43	0.68	2.69	2.89–5.05
7	14	6.05	5.28–6.41	5.96	0.87	4.83	4.61–7.53
8	17	7.99	7.63–8.35	8.02	0.84	7.02	6.50–9.69
M2							
1	7	1.31	1.21–1.45	1.34	0.13	1.00	1.15–1.48
2	3	1.73	·	1.97	0.45	1.59	1.69–2.49
3	9	3.23	2.89–3.31	3.00	0.42	2.34	2.19–3.37
4	1	(5.05)	·	(5.05)	·	(4.23)	·
5	4	4.84	4.67–5.49	5.08	0.66	4.83	4.61–6.04
6	17	6.92	6.19–7.53	6.80	0.87	5.66	5.28–8.15
7	10	8.24	7.69–8.97	8.38	0.81	7.65	7.14–9.69
8	0	·	·	·	·	·	·
M3							
1	2	3.11	2.99–3.23	3.11	0.17	3.20	2.99–3.23
2	1	(4.61)	·	(4.61)	·	(3.92)	·
3	10	6.12	5.05–6.92	6.06	0.98	4.67	4.73–7.69
4	4	7.39	6.65–7.84	7.25	0.88	6.88	6.65–7.84
5	8	8.06	7.68–9.10	8.31	0.88	7.65	7.14–9.69
6	1	(8.96)	·	(8.96)	·	(9.46)	·
7	0	·	·	·	·	·	·
8	0	·	·	·	·	·	·

[1] For each developmental stage (1–8) of the left mandibular I1–M3, the tables show the sample number of observations, 50th percentile age (median), interquartile range (25th–75th percentiles), mean age, standard deviation (SD), the midpoint age of attainment (MA; see text), and the age range observed. Dots (·) indicate that there was insufficient data for calculation, and parentheses () indicate single observations. All ages in years.

median age). Therefore, later stages of development (root vs. crown formation) for any tooth generally have larger SD's (and IQR's). To some degree, this observation may simply reflect the nature of different developmental stages—stage 1 by definition involves less calcification than stage 3, and may thus be inherently less variable in timing. However, stage 4 and stage 8 (crown and root completion, respectively) are also stages of short duration, but nevertheless tend to demonstrate relatively high variability compared to other stages. This tendency does not appear to be true for M_3—the SD's (and IQR's) for all M_3 stages are relatively high. These data thus reflect similar trends as those identified for human tooth development; there is greater variability in later-occurring events, and generally for the M_3 compared to other teeth (Garn et al., 1959; Chagula, 1960; Fanning, 1961; Moorrees et al., 1963; Bailit, 1976).

Figure 1 visually demonstrates the age variability associated with each developmental stage, as indicated by the interquartile ranges from Table 3. The age ranges for successive stages overlap for all teeth, although the median ages may be markedly disparate, depending on the teeth and stages examined.

Teeth can be divided into three groups based on the timing of initial crown calcification (stage 1): an early group composed of M_1, incisors, and canine; an intermediate group including premolars and M_2; and a late "group" including only M_3. Canine calcification is initiated early, but completion of the canine crown is delayed relative to the other teeth, and the canine and M_3 follow similar developmental schedules thereafter.

Age norms

Table 4 presents age norms for stages of tooth calcification for the total sample of chimpanzees, and for males and females separately. These "stage for age" tables show

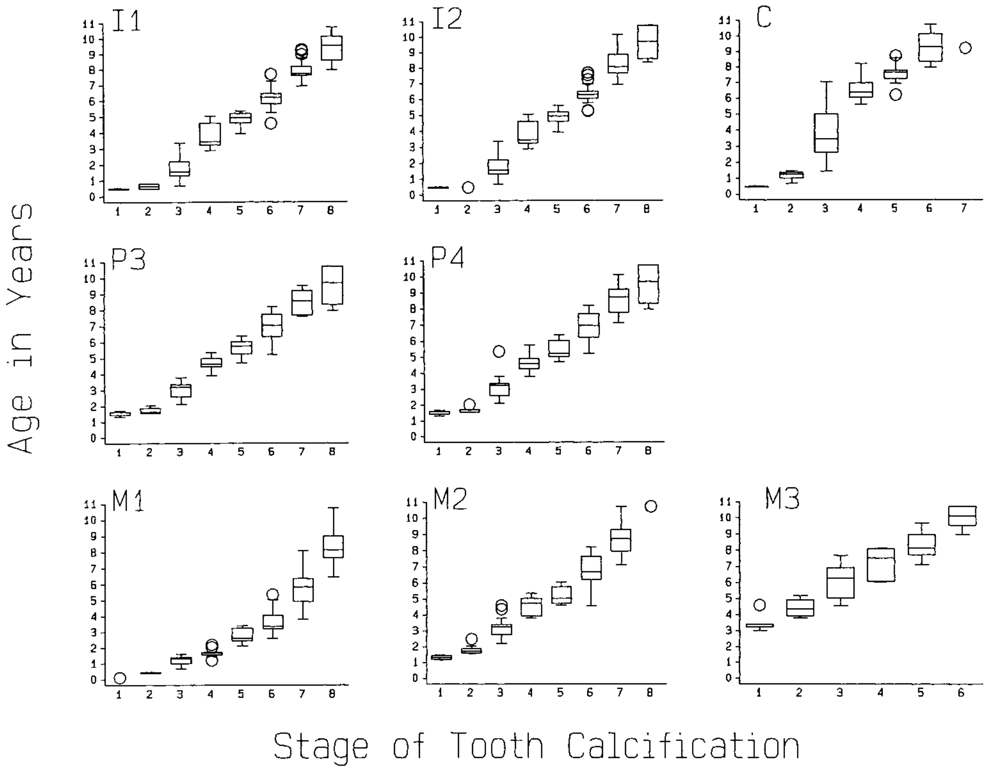


Fig. 1. Box plots demonstrating age variability in dental development stages for the left mandibular dentition (I1–M3). The line across the middle of each box represents the 50th percentile (median age); the box outline represents the 25th and 75th percentiles (interquartile range); the whiskers extend to the upper and lower adjacent values, defined as values within three-halves the interquartile range; values outside these limits are plotted as individual points (Computing Resource Center, 1989:187).

the modal (most commonly occurring) stage, and the range of stages found at given yearly age increments for each tooth. The developmental status of the entire dentition within a given yearly age category may be assessed by comparing modal stages, or the range of stages found, among tooth types.

Table 4 demonstrates that within a given yearly age class, any particular tooth type may exhibit a range of different developmental stages (maximum of 4 observed). This is again an indication of the variability characteristic of tooth development.

Although a difference in developmental stages between males and females is common for any given age class, there is no set pattern to the differences observed. *Either* males or females may be slightly advanced or retarded when a difference is discernable. The exception to this may be the canine, whose development is often retarded in males between 5 and 10 years of age.

Sex differences

Figure 2 shows high-low plots of data for crown and root calcification stages versus age in males and females. Despite the generally overlapping age distributions at a given stage, observable differences between males and females do exist. Males are generally older than females at stages 4 and 8 in I_1 and I_2. For the canine, males are generally older than females from stage 3 to stage 6. The same is found for P_3 at stages 7 and 8, M_1 at stage 5, M_2 at stage 7, and M_3 at stages 5 and 6. Females are occasionally observed to be older than males, for example at stage 6 in either incisor.

TABLE 4. *Age norms for stages of tooth development in chimpanzees*[1]

Age cateogry (years)	Data sample	I1	I2	C	P3	P4	M1	M2	M3
0–1	*T*	*1,3*	*3*	*1,2*	*0*	*0*	*2,3*	*0*	*0*
		0–3	*0–3*	*0–2*	*0*	*0*	*1–3*	*0*	*0*
	M	0	0,3	0,2	0	0	2,3	0	0
		0–3	0–1,3	0–2	0	0	1–3	0	0
	F	1,3	1,3	1	0	0	2,3	0	0
		1–2	1–3	1–2	0	0	2–3	0	0
1–2	*T*	*3*	*3*	*2*	*1*	*0*	*3*	*1*	*0*
		3	*3*	*2–3*	*0–2*	*0–2*	*3–4*	*0–2*	*0*
	M	3	3	2,3	2	0,2	3	2	0
		3	3	2–3	0–2	0–2	3–4	0,2	0
	F	3	3	2	1	1	3	1	0
		3	3	2–3	0–1	0–2	3–4	1–2	0
2–3	*T*	*3*	*3*	*3*	*3*	*3*	*5*	*3*	*0*
		3–4	*3–4*	*3*	*2–3*	*2–3*	*4–6*	*2–3*	*0–1*
	M	3	3	3	3	3	5	3	0
		3	3	3	2–3	2–3	4–6	2–3	0
	F	3	3	3	3	3	5	3	0
		3–4	3–4	3	3	3	4–6	2–3	0–1
3–4	*T*	*4*	*4*	*3*	*3*	*3*	*6*	*3*	*0*
		3–5	*3–5*	*3*	*3–4*	*3–4*	*5–7*	*3–4*	*0–2*
	M	4	4	3	3	3	6	3	0
		4–6	4–5	3	3–4	3–4	5–7	3–4	0–2
	F	3,4	3,4	3	3	3	6	3	0
		3–4	3–4	3	3	3	6	3	0–1
4–5	*T*	*4*	*4,5*	*3*	*4*	*4*	*7*	*4,5*	*2*
		4–6	*4–5*	*3*	*4–5*	*4–5*	*6–7*	*3–6*	*1–3*
	M	4	4	3	4	4	7	4	2
		4,6	4–5	3	4	4	6–7	3–4,6	1–3
	F	5	5	3	4	4	7	5	3
		5	5	3	4–5	4–5	7	5	2–3
5–6	*T*	*6*	*5,6*	*3*	*5*	*5,6*	*7*	*6*	*3*
		4–6	*4–6*	*3–4*	*4–6*	*3–6*	*6–7*	*4–6*	*2–3*
	M	5	5	3	4	5	7	5	3
		5–6	5–6	3	4–6	3–6	6–7	4–6	2–3
	F	6	6	3	5	6	7	6	3
		4–6	4–6	3–4	5	5–6	6–7	4,6	3
6–7	*T*	*6*	*6*	*4*	*6*	*6*	*7*	*6*	*3*
		6–7	*6–7*	*3–5*	*5–6*	*5–6*	*7–8*	*5–6*	*3–4*
	M	6	6	3	6	6	7	6	3
		6	6	3–4	6	6	7–8	6	3–4
	F	6	6	4	6	6	7	6	3
		6–7	6–7	4–5	5–6	5–6	7–8	5–6	3–4
7–8	*T*	*7*	*7*	*5*	*6*	*6*	*8*	*6*	*5*
		6–8	*6–7*	*3–6*	*6–8*	*6–8*	*7–8*	*6–7*	*3–5*
	M	7	7	5	6	6	8	6	3
		7	7	3,5	6	6–7	7–8	6–7	3–4
	F	7	7	5	6	6	8	6	5
		6–8	6–7	4–6	6–8	6–8	7–8	6–7	3–5
8–9	*T*	*7*	*7*	*5,6*	*6*	*7*	*8*	*7*	*5*
		7–8	*7–8*	*4–6*	*6–8*	*6–8*	*7–8*	*6–7*	*4–6*
	M	7	7	5	6	6,7	8	6,7	5
		7–8	7–8	4–5	6–7	6–7	7–8	6–7	4–5
	F	7	7	6	6,7,8	7	8	7	5
		7–8	7–8	5–6	6–8	6–8	8	6–7	4–6
9–10	*T*	*7,8*	*7*	*6*	*7*	*7*	*8*	*7*	*5*
		7–8	*7–8*	*6–7*	*7–8*	*7–8*	*8*	*7*	*5–6*
	M	7,8	7	6	7	7	8	7	5,6
		7–8	7	6	7	7	8	7	5–6
	F	7,8	7,8	6,7	7,8	7,8	8	7	5
		7–8	7–8	6–7	7–8	7–8	8	7	5
10–11	*T*	*8*	*8*	*6*	*8*	*8*	*8*	*7*	*6*
		8	*7–8*	*6*	*8*	*7–8*	*8*	*7–8*	*6*
	M	8	8	6	8	8	8	7	6
		8	7–8	6	8	7–8	8	7–8	6
	F	·	·	·	·	·	·	·	·
		·	·	·	·	·	·	·	·

[1] By yearly age categories, the data are presented for the total sample (*T*; in italics), males (M), and females (F). The two rows for each sample (*T*, M, or F) show the modal stage (top) and range of stages (bottom) found for each tooth at each age category. There may be more than one "modal" stage, defined as the stages occurring at the highest frequency in a particular age class. A dot (·) indicates that no observations exist for the particular tooth-age category combination.

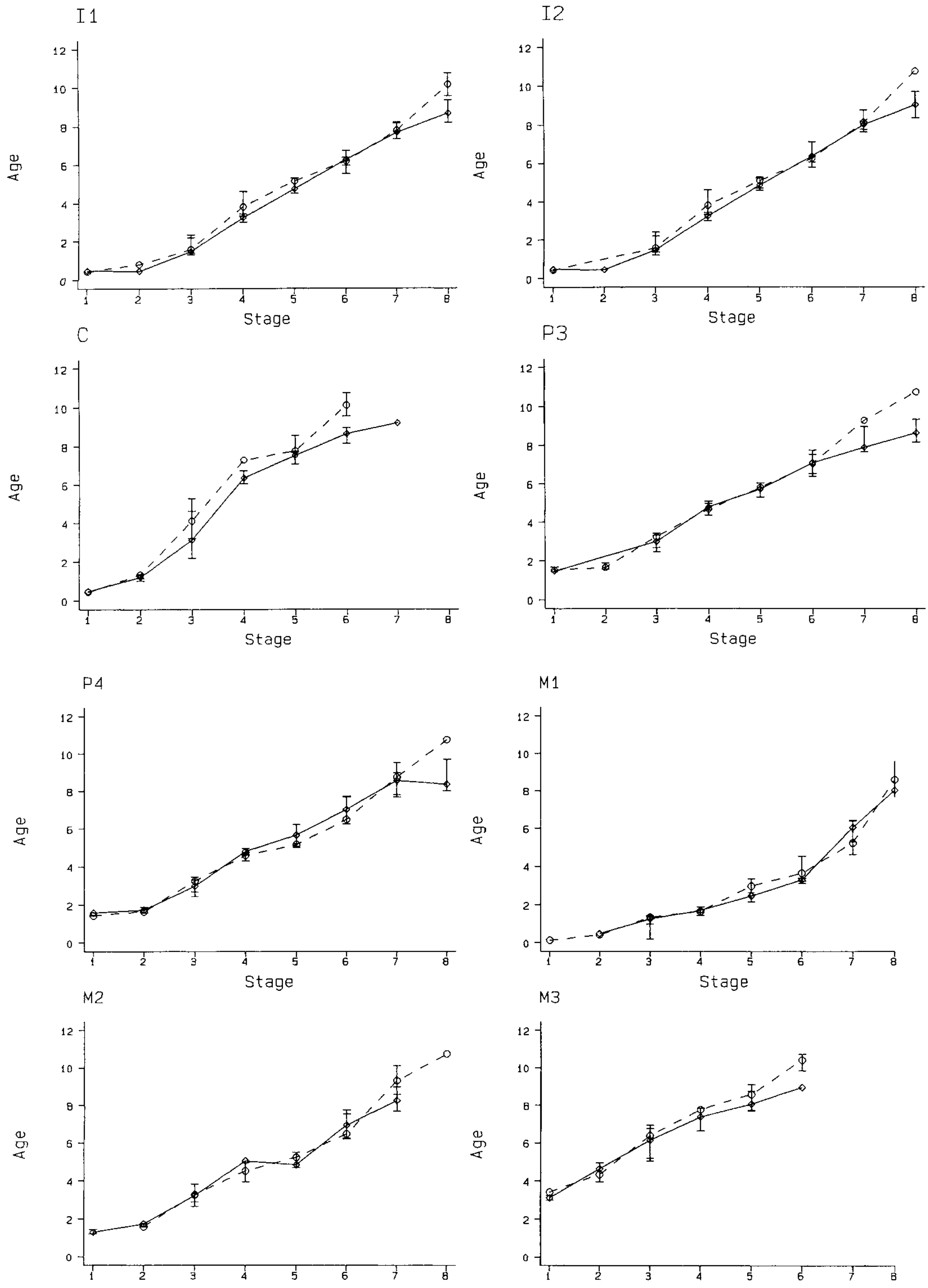


Fig. 2. High-low plots demonstrating sex differences in timing for chimpanzee tooth development in the left mandibular I1–M3. Bars represent the interquartile range, and the symbols (circles = males; diamonds = females) locate the median age for each stage. Dashed lines connecting symbols represent males, solid lines represent females. Data from Table 3b,c.

Using the Wilcoxon rank-sum test, statistically significant differences ($P < 0.05$) in age were found for males and females exhibiting canine development at stage 3 ($P = 0.034$), stage 5 ($P = 0.021$), and stage 6 ($P = 0.018$); P_3 at stage 8 ($P = 0.034$); and M_1 at stage 5 ($P = 0.034$). In all of these comparisons, males were significantly older than females.

The only statistically significant sex difference using the Bonferroni correction ($P < 0.0063$) was for the canine at stage 6 ($P = 0.0061$). As in the Wilcoxon tests, males were older than females at this stage.

Age prediction models

Regression models of age on dental maturity (DM and Dm) and their estimated 95% confidence limits for predicted age are shown in Figure 3a,b (see figures for regression equations).

The differrence in the error term between the model using M_3 and that omitting M_3 was negligible (0.92 years versus 0.99 years), suggesting that the M_3 has little value for age prediction. The developmental timing of human third molars is well known to be extremely variable (Garn et al., 1958b, 1959, 1961; Chagula, 1960; Fanning, 1961; Moorrees et al., 1963; Thompson et al., 1974). Additionally, the error range in both models approaches two years, obviously limiting the accuracy of age predictions using this method. However, predicted ages from tooth calcification status are more accurate (i.e., have a smaller error term) than those estimated from tooth *emergence* scores by Kuykendall et al. (1992). Estimates for two standard deviations at the mean number of emerged permanent teeth was ± 1.63 years in the left mandibular quadrant, versus ± 0.92 years for the comparable model above using a dental maturity score. The presence of such wide ranges of normal variability implies that overly precise age estimates are unrealistic.

Duration of crown and root formation

Figure 4 is a comparison of crown and root formation periods in chimpanzees and humans. The duration of crown formation of each tooth is shown below the zero line, and that for root formation above. Figure 4 compares two developmental features for each tooth—the absolute duration of crown or root formation (in years; the duration of crown formation was calculated as the difference between median ages for stages 1 and 4, and that for root formation as the difference between stages 4 and 8), and the proportion of crown vs. root formation. The former is indicated by the length of each bar below or above the line, the latter by the ratios indicated for each tooth in both species (see methods).

Data for the duration of chimpanzee tooth crown and root development are from this study and supplemented by Anemone et al. (1991) and Anemone and Watts (1992). Since the ages for root completion in this study may be biased by the four oldest chimpanzees in this sample (see discussion below), root completion ages (in chimpanzees) used to construct Figure 4 represent averages between this study and those cited.

Estimates used for humans were calculated as averages of mean and median ages for relevant stages of tooth development published by Garn et al. (1958a, 1959), Moorrees et al. (1963), Fanning and Brown (1971), and Harris and McKee (1990). For incisors, crown initiation ages are only available from Schour and Massler (1940, 1941), the limitations of which are discussed below. Although these may be considered rough estimates, they are more appropriate as species parameters than are estimates from any single human population.

The ratios included in Figure 4 represent the relative proportions of crown and root developmental periods in each tooth, and are calculated as (time for crown development)/(time for root development) (both in years). Thus, ratios greater than one indicate teeth in which crown development occupies a longer period, and those less than one indicate teeth with longer periods of root formation.

The bar graphs indicate that the overall periods (crown + root calcification) occupy similar amounts of time in chimpanzees and humans for incisors and canines, but not for the postcanine teeth. Crown formation in human incisors, M_1 and M_2, takes longer than that in chimpanzees, while chimpanzee canine crown formation takes longer than

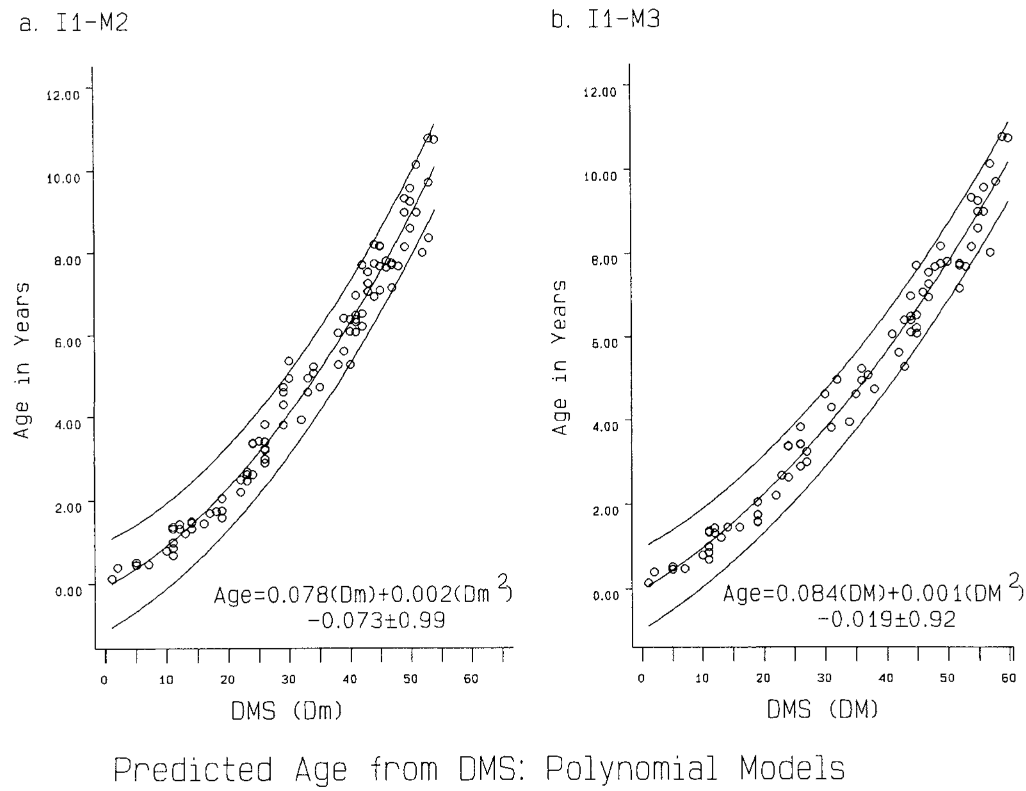


Fig. 3. Polynomial regression models for age prediction from dental maturity score (circles), based on a *squared* transformation of dental maturity (DM) score. In **a**, Dm was calculated as the summed developmental stages of the left mandibular I1–M2; in **b**, DM is the sum of I1–M3. Each graph shows the predicted regression line and estimated 95% confidence bands. The age prediction formulae are included for each model.

that of human canines. Crown formation periods in the premolars and M_3 are roughly equivalent in both species.

Root formation of chimpanzee incisors appears to occupy a slightly greater period than for human incisors, but given the nature of these estimates, this difference is questionable. Human root formation takes a longer period of time compared to chimpanzees in all other teeth.

The molars are the only teeth demonstrating greater periods of both crown and root formation in humans compared to chimpanzees. Note that the mesial-to-distal increase in timing for the development of molar crowns and roots described by Anemone et al. (1991) occurs only for crown formation in chimpanzees; the root formation period in M_3 for both species, and that of crown formation in humans, appears to be no greater than that for M_2.

Although the absolute durations of tooth formation are in some cases quite similar, the dissimilarity in chimpanzee and human crown:root ratios indicates that relative differences in development exist for some teeth.

For example, the crown:root ratios indicate that incisor crown formation in chimpanzees occupies approximately twice the time as that allotted to incisor root growth. In humans, these periods are equivalent. The crown formation period in chimpanzee canines is greater than that of root formation, but the crown formation period in human canines is only half that of the root. Root formation in premolars takes longer than the crowns in both species, but the chimpanzee ratios are closer to 1.0 (i.e., the

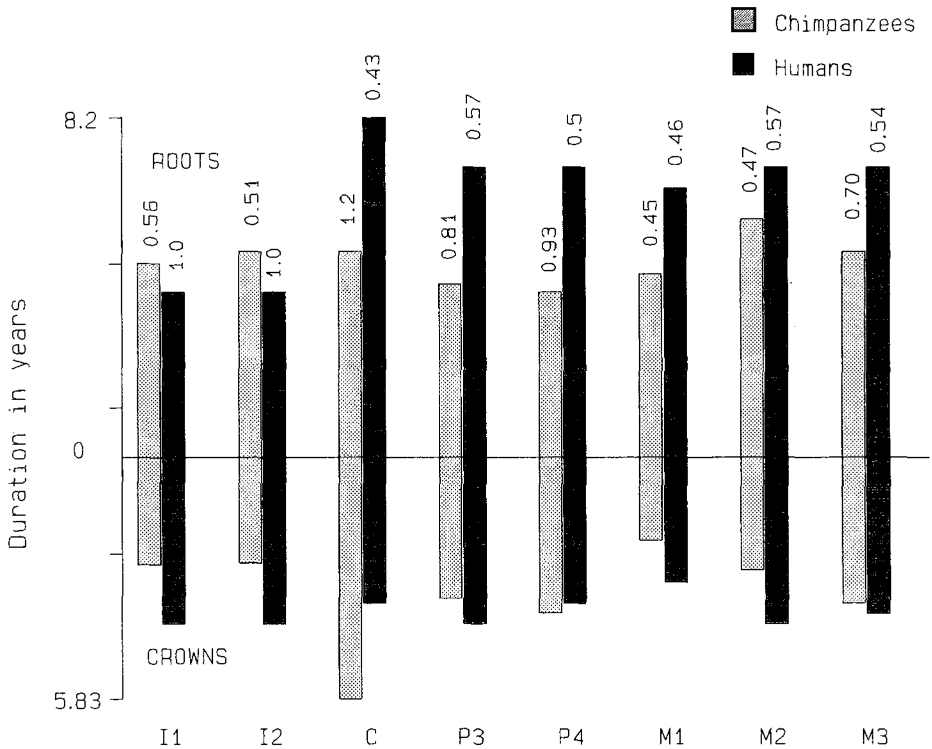


Fig. 4. Crown and root formation periods in chimpanzees and humans. Crown formation is represented by bars below the zero line, and root formation by those above. As described in the text, each bar represents the estimated duration of crown or root formation for a particular tooth. Ratios above each bar represent the relative proportions of crown and root developmental periods in each tooth: (time for crown development)/(time for root development).

duration of crown and root periods are more similar). Finally, the ratios for all molars are very similar in both species, indicating that the differences observed in chronological time are proportional in relative time.

DISCUSSION

Results presented here generally agree with those previously published for dental development in great apes, especially with Anemone et al. (1991) and Anemone and Watts (1992). Other studies are not directly comparable. Dean and Wood (1981) utilized published tooth *emergence* ages for pongids to establish a dental development chronology. Simpson et al. (1990, 1991, 1992) analyzed relative dental development relationships, but did not present age estimates.

Anemone et al.'s (1991) chimpanzee dental development standard was the first derived from a living ape population. They did not estimate actual *median* age estimates for stages of tooth crown and root calcification, but minimum ages and age ranges for crown initiation, crown completion, and root completion were given. However, Anemone and Watts (1992) published "median age" estimates for all stages of molar tooth formation from the same study population. These estimates and age ranges (from Anemone and colleagues) are summarized in Table 5. Most are rather general estimates (not actually medians), calculated only to the nearest year due to the variability in the inter-exam intervals during the original data collection (Anemone et al., 1991). They generally approximate the age of first appearance of a given tooth development stage, and are most comparable to the MA age estimates in this study.

Given the differences between study samples and methods, the degree of similarity

TABLE 5. "Median" ages of first appearance and ranges for tooth development stages in chimpanzee incisors, canines, and premolars (Anemone et al., 1991) and molars (Anemone and Watts, 1992)[1]

Stage	I1	I2	C	PMs	M1	M2	M3
A(1)	0.66	0.75	1.25	1.75	0	1.5	3.5
B(2)	·	·	·	·	0.83	2	6
C(3)	·	·	·	·	1.5	3	7
D(4)	3.1	3.1	7	6	2	4	7
E(5)	·	·	·	·	2.75	6	9
F(6)	·	·	·	·	3.25	7	10
G(7)	·	·	·	·	4	8	11
H(8)	7	7	12	9.5	5	9	12

[1] For most teeth, ages are only available for crown initiation (stage A), crown completion (stage D), and root completion (stage H). Numeric equivalents used in this study are given in parentheses.

between these and previous results [most notably Anemone et al. (1991) and Anemone and Watts (1992)] is in fact striking. However, the differences in this study compared to Anemone and colleagues include a) root completion in incisors is achieved later; b) canine crown initiation begins earlier; c) premolar crown completion is achieved earlier; and d) root completion in the molars is achieved later.

Some of these differences can perhaps be explained in terms of methodological and sampling factors, including inter-observer differences in the criteria used to assess developmental stages such as root apical closure, and the fact that this study is cross-sectional and the previous is longitudinal. Differences in sample size (n = 118 vs. 16) and age structure of the samples also appear to affect estimates.

This applies in particular to the final stage of root completion (stage 8). The age estimates for stage 8 in this study are considerably older for some teeth. In fact, the estimates from Anemone and colleagues are younger than the lower limit of the age ranges of stage 8 for the incisors, M_1, and possibly M_2 (compare Table 5 with Table 3a). Unlike earlier stages, root completion (stage 8) has no succeeding stages which naturally limit the upper age range. Therefore, in cross-sectional assessment (presence-absence), the upper age limit for the completion of tooth formation may be biased upward since it is not known when the oldest animals in the sample actually attained root completion. This may explain the high SDs obtained for root completion in all teeth. Also, since this study population has small samples for the two oldest age groups (n = 5 for 9–10 years; n = 4 for 10–11 years), the attainment of root completion (only) may be more accurately estimated from longitudinal data, especially if a correction factor is applied (see Dahlberg and Menegaz-Bock, 1958; Bailit 1976). Thus, the "true" median estimates for incisor, M_1, and M_2 root completion probably fall somewhere between those from this study and previous estimates (i.e., Anemone et al., 1991; Anemone and Watts, 1992).

Finally, some of the observed age differences may simply illustrate that the full range of normal variation in tooth development is greater than either study could document alone.

A general sketch of the timing of tooth development events in the chimpanzee can thus be described using age estimates and ranges from all available sources (Fig. 5). Both incisors follow similar schedules, with crown formation beginning at approximately 0.5 years, and ending at 3–3.5 years. Incisor root formation continues from this point until at least 7 years (Anemone et al., 1991), and as late as 8.6 years in I1, and 9.2 years in I2 (this study). The canine begins crown formation at the same age as the incisors, or as late as 1.25 years (Anemone et al., 1991), and crown completion occurs between 6 and 7 years. Canine root completion occurs at approximately 12 years (Anemone et al., 1991). The premolars begin crown formation at approximately 1.5 years (1.4–1.8), complete crown formation at either 6 years (Anemone et al., 1991), or rather earlier at about 4 years (this study). P4 is somewhat later than P3 in crown completion. Premolar root formation is completed at about 9–9.5 years. The first molar may begin crown formation prenatally as it has been observed

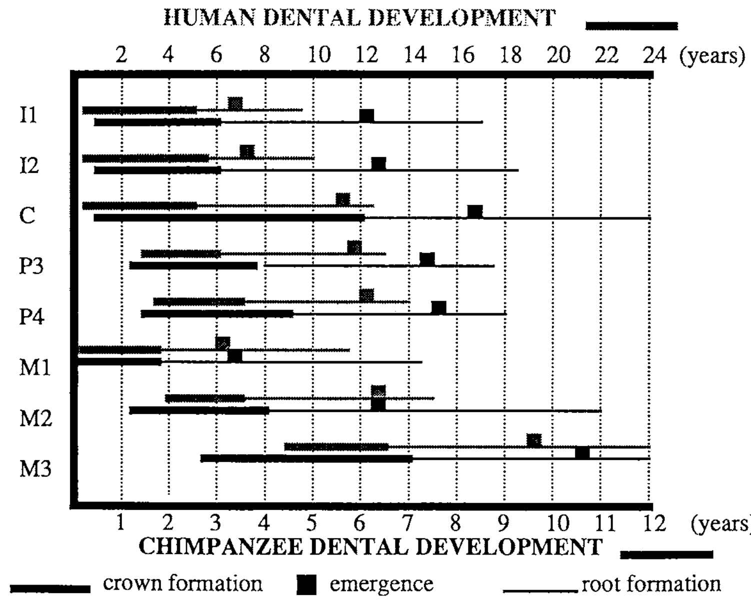


Fig. 5. Dental development standard for chimpanzees (bottom) and humans (top). For each tooth, the period of crown formation is represented by the heavy solid line, and root formation by the fine line. The timing of tooth emergence is indicated by the solid blocks, utilizing median gingival emergence ages from Kuykendall et al. (1992). Human data from sources cited in Anemone et al. (1991).

radiographically on the first day following birth in chimpanzees and other great apes (Swindler, 1985; also Beynon et al., 1991; Siebert and Swindler, 1991; Winkler et al., 1991). Crown completion in M_1 is achieved before 2 years of age, and root formation is completed either at about 5 years (Anemone and Watts, 1992), or later at just over 7 years (this study). The second molar begins crown formation by 1.5 years or slightly earlier, exhibits crown completion at about 4 years, and root completion at 9 years or later. The third molar does not begin crown formation until about 3.5 years, and crown completion occurs at about 7 years. Finally, root completion in the M_3 occurs at about 12 years (Anemone et al., 1991).

From these results, a revised comparison of tooth developmental events for both chimpanzees and humans is presented in a format similar to that employed by Dean and Wood (1981), Swindler (1985), Anemone et al. (1991), and Smith (1991a) (Fig. 5). Data for phases of crown and root formation are taken from Table 3, defined by the MA ages (midpoint age of attainment) for stages 1 and 4 (crown formation), and stages 4 and 8 (root formation). Tooth emergence ages for chimpanzees (indicated by solid blocks) are from Kuykendall et al. (1992), and are derived from mixed-longitudinal dental emergence records from the LEMSIP population.

Sex differences in chimpanzee tooth formation

Sex differences in tooth development timing in chimpanzees and other apes have been minimized in previous accounts. But both absolute and relative differences in tooth emergence have been reported (Krogman, 1930; Schultz, 1935; Nissen and Reisen, 1964), and usually involve the canine. Such differences are always considered to be "not significant," and it is often reported that they simply do not exist in apes (Dean and Wood, 1981; Dean, 1985; Simpson et al., 1990). The results from the present study conflict with these views.

Although sex differences in tooth formation timing were identified for several teeth at certain stages of development, the Bonferroni tests indicate that such differences

achieve statistical significance only for the canine at stage 6. The difference in mean age between male and female chimpanzees demonstrating stage 6 in the canine is 1.4 years. This difference for stages 3–5 in the canine ranged from 0.64 to 0.94 years (stage 4 was not found to achieve statistical significance from the Wilcoxon results, but there were only two males and eight females; it is perhaps due to the uneven sample sizes). Most other differences in mean age between males and females, at any stage and for any tooth, ranged from 0.0003 to 0.5 years. Only a few stages among all other teeth showed mean age differences comparable to this "canine range," for example the P3 at stage 7 (0.92 years) and M_1 at stage 5 (0.63 years). Notably, the canine is the only tooth demonstrating sex differences in age of such magnitude over several consecutive stages. In contrast to previous studies, these patterns of sex differences suggest that there may be biologically meaningful differences in canine developmental timing between male and female chimpanzees.

Furthermore, since these sex differences were not found in the earlier stages of crown formation, it appears that the period of formation of the larger male canine crown is prolonged, rather than "delayed" as commonly reported, compared to females. The period of crown calcification (calculated as the difference in MA ages for stage 1 and stage 4) is approximately 5 years in females, versus 6.3 years in males. Although the attainment of subsequent developmental stages appears to be delayed in males (i.e,. ages are later), this is an expected consequence of prolonged male canine crown formation. However, the manifestation of sexually dimorphic differences may involve differences in rate, duration, and timing of developmental processes (Shea, 1983), and longitudinal data are required to properly elucidate these differences in chimpanzees.

Canine development

The results presented here indicate that the timing of initial crown calcification in canines, incisors, and first molars is very similar in chimpanzees and humans, as concluded by Swindler (1985) and Anemone and Watts (1992). In contrast, Simpson et al. (1990, 1991, 1992) concluded that human canine calcification is significantly advanced relative to other teeth, showing "an incisor-like onset" (1990, p. 290) in contrast to the chimpanzee canine. Their relative developmental comparisons indicate that initial calcification of chimpanzee canines is significantly delayed relative to that of the incisors and M_1. There are ample data available with which to refute this conclusion. For initial canine crown calcification in humans, Moorrees et al. (1963) and Fanning and Brown (1971) published mean and median age estimates, respectively, ranging between 0.4 and 0.7 years for males and females. Initial M_1 calcification in humans is generally detectable at birth (Gleiser and Hunt, 1955; Garn et al., 1959; El-Nofely and Iscan, 1989), and other studies also document early initial M_1 calcification at 0.1–0.3 years (Garn et al., 1958a; Moorrees et al., 1963; Fanning and Brown, 1971).

Initial incisor calcification in humans also occurs early in postnatal life, but has not been precisely documented in most studies. Schour and Massler (1940, 1941) documented the beginning of mandibular incisor calcification at 4–6 months of age (0.3–0.5 years), and at 10–11 months (0.8–0.9 years) for maxillary incisors. Although results from that study have been criticized on the basis of its small sample size and the use of developmentally abnormal specimens (Garn et al., 1959; Miles, 1963; Demirjian, 1986; Smith, 1987b), recent results by Liversidge et al. (1993) provide confirmation of these ages. Initial mandibular incisor calcification was documented in their analysis at 0.4 years; the maxillary second incisor was later, at 1.1 years.

In chimpanzees, Anemone et al. (1991; Anemone and Watts, 1992) documented the presence of canine calcification in two individuals in their sample at 12–15 months of age (1.0–1.3 years). M_1 calcification in the chimpanzee has been documented before birth (Oka and Kraus, 1969; Tarrant and Swindler, 1972; Swindler, 1985; Siebert and Swindler, 1991), and between 1 day and 3 weeks of age (Anemone et al., 1991). Initial calcification of the incisors was documented between 6 and 8 months (0.5–0.7 years) in the latter study. Results for chimpanzees in

this study yield nearly identical age estimates for initial canine and incisor crown calcification: stage 1 in I1, I2, and canine occurred within the first 6 months of age (50th percentile at 0.48 years; age range 0.45–0.51; n = 3 for incisors, n = 4 for canine). Initial crown calcification in M_1 was observed at 0.13 years (n = 1). In sum, the incisors, canine, and first molar begin development at similar times in terms of both the absolute and relative timing in chimpanzees and humans. Further discussion of canine development is given below.

Crown and root formation periods in chimpanzees and humans

Comparative studies to date have identified similarities and differences in chimpanzee and human dental development periods on both absolute and relative time scales (Dean and Wood, 1981; Simpson et al., 1990, 1991, 1992; Anemone et al., 1991; Anemone and Watts, 1992; Kuykendall and Conroy, 1993). The situation is complex. Because of the difference in overall periods of growth and development in chimpanzees and humans, similarity in the chronological timing (of the duration or initiation of stages) of tooth crown and root developmental periods often equates with relative developmental differences between chimpanzees and humans. However, differences in absolute timing may be proportional, and thus may not involve relative differences. Therefore, a straight comparison of the chronology of chimpanzee and human dental development is not particularly useful; developmental periods must be compared on relative terms. Nevertheless, it is important to know that certain periods of tooth formation in chimpanzees and humans are of equivalent duration despite tooth size differences, as this *does* give us insight into dental development processes in different species.

For example, the overall tooth developmental periods (crown plus root formation) of the chimpanzee and human canines are of nearly equivalent duration (given appropriate error ranges for the estimates utilized). But the larger chimpanzee tooth possesses a longer period of crown calcification, both on the chronological scale, and relative to root formation (ratio = 1.2 vs. 0.43 in humans). Therefore, relatively less time is devoted to chimpanzee canine root formation compared to humans.

The developmental mechanism allowing the larger chimpanzee canine to develop in an equivalent amount of time as compared with the smaller human tooth might involve at least two factors. First is the shift in proportions of the developmental period allotted to crown and root formation, as indicated by Figure 4. The second is a microstructural feature of teeth. Differing orientations of the incremental lines in dental hard structures of ape and human teeth have been documented, and may explain the higher rate of tooth calcification observed for larger ape teeth (Dean and Wood, 1981; Dean, 1985). In the light of such factors, and with the observation that initial crown formation occurs relatively early in both chimpanzees and humans, it may not be proper to describe development of the chimpanzee canine as "delayed" relative to the human canine. This is an oversimplication which does not properly describe the complex processes involved, and contributes little to our understanding of the differences between chimpanzee and human development or life history.

A final issue concerns conflicting views of the nature of developmental differences between the molar teeth in chimpanzees and humans. The more accepted view claims that the prolongation of molar development in humans is distinctively reflected in the developmental patterns between chimpanzees and humans (Mann, 1975; Mann et al., 1987; Anemone et al., 1991; Anemone and Watts, 1992). However, Smith (1987a) considered these differences to be less significant than previously claimed, and Simpson et al. (1990, 1991, 1992) found no significant differences in relative developmental patterns among the postcanine teeth of apes and modern humans [but see Anemone and Watts (1992) for critical commentary on their methods].

Although differences do appear to exist between chimpanzee and human patterns of molar development, Kuykendall and Conroy (1993) concluded that they are too ambiguous to allow distinctions between species. This is due in part to the amount of variation present in both species, but also because of

the lack of adequate comparative data. These conflicting conclusions may in part stem from sampling and methodological differences among studies (e.g., longitudinal vs. cross-sectional samples, methods for calculating ages, used of unaged crania, and whether particular studies actually determine developmental sequences among individuals or construct sequences from mean or median ages).

It is also possible that the complexity of dental development processes is interfering with the elucidation of interspecific differences among molar developmental patterns. While there is no doubt that molar development in humans is prolonged compared to chimpanzees, it is not clear how this feature affects the relative developmental relationships among teeth. For example, Anemone et al. (1991) identified a mesial-to-distal trend for longer crown development among chimpanzee molars. They cited data identifying a similar trend in humans (Moorrees et al., 1963), macaques (Sirianni and Swindler, 1985), and *Cebus albifrons* (Fleagle and Schaffler, 1982). A close look at the available data indicates that humans differ slightly from this trend.

As shown in Results, molar crown development periods in chimpanzees demonstrate a straight increase progressing from M_1 to M_3, but human molar crown periods increase from M_1 to M_2, and may actually decrease for M_3 (Fig. 4). In both chimpanzees and humans, molar *root* development periods also show an increase for M_1–M_2, followed by a decrease or levelling off for M_3. Thus the pattern is not a simple mesial-distal increase.

Crown and root formation patterns of molars do differ in chimpanzees and humans, but the crown:root period ratios indicate that root formation in both chimpanzees and humans occupies a greater proportion of "molar developmental time" than does molar crown formation (i.e., the ratios are all less than 1.0). Therefore, chimpanzee and human molars do differ both in absolute and relative timing of their developmental periods, but the differences are not as great as those observed for other teeth (e.g., differences between crown:root ratios are greater), and they alone do not clearly distinguish between chimpanzee and human dental development patterns.

One possible (though still speculative) explanation for such developmental differences is that they are related to relative molar size in chimpanzees and humans. The molar size progression (in mesial–distal length) in chimpanzees is M1 < M2 > M3, while that for human molars is M1 > M2 > M3 (Swindler, 1976). Additionally, microstructural differences relating to the orientations of incremental lines in dental hard tissues may be involved, as explained above for the canine.

CONCLUSIONS

There is a steadily increasing volume of data concerning primate and human growth and development which is invaluable for formulating models of the evolution of "human" life history. However, as new data allow, general comparisons must be replaced with more detailed analyses, and dental development data must be incorporated (where appropriate) into studies of growth and development of other bodily systems, such as craniofacial growth and morphology. Comparisons of dental development alone have limited value for studies of early hominid life history or evolution, but the dentition remains the most widely used and most accessible growth marker applicable to fossil analysis.

To this end, the data presented here constitute a baseline for further study and comparison between species. In contrast to previous studies, sex differences were detected in the timing of stages of canine tooth development. Comparison of tooth formation periods reveal that all teeth exhibit developmental differences between chimpanzees and humans, but that these are greater in the incisors, canine, and premolars than in the molars.

Like the growth and development period overall, the dental development period in humans is prolonged compared to chimpanzees. However, on a general level, the prolonged growth period in humans may be seen as the extension of a trend characteristic of all primates; humans simply demonstrate the extreme (Schultz, 1935, 1950, 1960;

Watts, 1985). Additionally, the relative similarity in proportions of growth periods, including those of dental development, has been well documented among primates (Schultz, 1935, 1960; Gavan and Swindler, 1966; Dean and Wood, 1981; Swindler, 1985). That humans demonstrate features characteristic of "primate" growth and development is as important to acknowledge as are the differences which have been documented between humans and other primate species.

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